



Lethal and sub-lethal responses of rocky shore gastropods to extreme temperatures

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ABSTRACT

Intertidal communities are more frequently experiencing extreme air and sea temperatures as a result of anthropogenic climate change, with heatwaves increasing in intensity and duration. Most studies exploring the thermal tolerances of intertidal species to extreme temperatures haven't directly studied early life stages. We explored whether locally extreme tide-out temperatures were lethally impacting premature Boreal (*Littorina littorea* and *Steromphala cineraria*) and Lusitanian (*Phorcus lineatus* and *Steromphala umbilicalis*) intertidal gastropod species from southwest England. Two separate experiments tested lethal and sub-lethal responses to simulated local heatwave and cold spell temperatures. Two sensitive early size classes (new recruits and year 1+ juveniles) for each species were exposed to simulated extreme and ambient tide-out temperatures in replicated boulderfield (air) and rockpool (seawater) microhabitats per experiment. Realistic experimental temperatures were determined by EnvLogger temperature data recorded locally in sun-exposed, shaded and rockpool intertidal habitats. For each nine-day experiment, specimens were exposed for six hours daily to four laboratory thermal treatments simulating both ambient conditions and extreme temperature events. These experiments were designed to test the following questions: are premature trochids and littorinids more sensitive to extreme temperatures than adults, and is there a difference in response between species of Boreal and Lusitanian origin sampled from the same geographical region? We identified that the premature intertidal trochid species may not be more thermally sensitive than adults, although premature *L. littorea* may have a slightly lower lethal heat limit. Survivorship in extreme heatwave air temperatures (40.0–42.9 °C) was lowest for lowshore and highest for highshore species, relating directly to species' vertical shore zonation. There were minimal to zero mortalities in all other thermal treatments. Following stress-induced inactivity in the extreme heatwave air temperature treatment, *S. cineraria* and *P. lineatus* specimens all died. In contrast, *L. littorea* and *S. umbilicalis* specimens recovered in some instances. Intensifying and more frequent aerial heatwave events occurring unseasonably are likely to cause population declines, local extinctions or subtidal retreat for premature lowshore Boreal intertidal species, influencing recruitment to adult populations, especially where rockpools are not present to provide thermal refugia. Conversely, mid-highshore Lusitanian species are likely to be more resilient to high air temperatures during low tides. Cold spell temperatures did not lethally or sub-lethally impact any juvenile gastropod species, suggesting Lusitanian species will thrive as a result of increasingly milder winters.

1. Introduction

In intertidal ecosystems, organisms are subjected to alternating conditions typical of both marine (tide-in) and terrestrial (tide-out) environments. These conditions vary with latitude (Mieszkowska et al., 2021), along the vertical intertidal gradient, across tidal cycles and

seasons (Helmuth et al., 2006), and amongst microhabitats generated by both topography (Lima et al., 2016; Seabra et al., 2011; Seabra et al., 2015) and habitat forming species (Moore et al., 2007). This creates one of the most challenging habitats for marine organisms (Raffaelli and Hawkins, 1996). These natural stressors are, however, intensifying due to anthropogenically-induced climate change (ACC). Gradual increases

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in air and seawater temperatures are the result of ACC across much of the globe, although some regions are experiencing localised sea surface temperature cooling from amplification of wind-driven upwelling (Cooley et al., 2022; Hoegh-Guldberg et al., 2014) and a weakening of the Atlantic Meridional Overturning Circulation (AMOC) (Caesar et al., 2018). Furthermore, both marine (Cooley et al., 2022; Hoegh-Guldberg et al., 2014; Holbrook et al., 2020; Mieszkowska et al., 2021; Oliver et al., 2018) and atmospheric (Hoegh-Guldberg et al., 2018; Parmesan et al., 2022; Prodhomme et al., 2022) extreme heatwave events are rapidly increasing in frequency. Although predicted to decrease in global frequency (Clarke et al., 2022; Diffenbaugh et al., 2005; Yao et al., 2022), winter 'cold spells' are also a feature of ACC (Palmer, 2014), with extreme cold events punctuating increasingly milder winter air and sea temperatures that are being experienced in the mid-latitudes of the northern hemisphere (Cohen et al., 2014; Firth et al., 2015). In contrast, AMOC weakening may impact the northern hemisphere through increased intensity of cold spell events over parts of North America (Yin and Zhao, 2021), yet northern Europe is likely to experience fewer winter cold spell events despite regional cooling of mean surface temperatures (Meccia et al., 2024).

The coldest winter air temperatures for 30 years occurred in the British Isles and Ireland during 2009/2010, with the following December (2010) becoming the second coldest for 350 years (Blunden et al., 2011; Capstick and Pidgeon, 2014). Conversely, some of the hottest summer air temperatures on record have occurred over the last decade. The July heatwave of 2022 in the British Isles resulted in a new record air temperature of 40.3 °C (MET Office, 2022; Yule et al., 2023), with the highest ever daily global mean surface air temperature recorded in July 2023 (ECMWF: The copernicus programme, 2023).

Extreme temperature events can lethally impact intertidal communities. Heatwaves, resulting in rapid and unprecedented increases in air and seawater temperatures, have been shown to cause mass mortalities in rocky shore species (Garrabou et al., 2009; Harley, 2008; Hesketh and Harley, 2023; Mieszkowska et al., 2021; Oliver et al., 2018; Tsuchiya, 1983; Williams and Morritt, 1995). They are particularly stressful for sessile ectothermic organisms (Mislan and Wethey, 2015). Repeated exposure to heat stress has been shown to decrease thermal tolerances in the blue mussel, *Mytilus edulis* (Linnaeus, 1758) (Jones et al., 2009; Seuront et al., 2019). Conversely, research has also demonstrated that brief heat stress might actually increase temperature tolerances in intertidal species (Moyen et al., 2020; Zhang et al., 2021). Studies on the upper thermal tolerance limits of different life stages of intertidal organisms have found mixed results in regards to thermal vulnerability of larvae/juveniles, showing some as more vulnerable to high temperatures (Crisp and Ritz, 1967; Pandori and Sorte, 2021; Truebano et al., 2018), as equally sensitive to thermal stress as adults (Pechenik et al., 2019), or even exhibiting high thermal resistance in comparison to adults of the same species (Diederich and Pechenik, 2013; Tangwancharoen and Burton, 2014). During a cooler period in the northeast Atlantic in the 1960s to early 1980s (Philippart et al., 2011), winter cold temperatures influenced the survival rates of newly settled juvenile intertidal ectotherms towards northern range limits (Bowman and Lewis, 1986; Lewis et al., 1982) and in some extreme cold winter cases, the survival rates of adults (Crisp, 1964).

Desiccation tolerance is another limiting factor setting upper zonation limits on rocky shores (Raffaelli and Hawkins, 1996), inextricably linked to intertidal species thermal tolerances during low tides. Unlike sessile organisms, mobile intertidal ectotherms use behavioural buffering (Ng et al., 2017) to seek out thermal refugia away from extreme hot temperatures to avoid desiccation (Chappon et al., 2017; Lima et al., 2016), and cold temperatures to avoid freezing (Moisez et al., 2020; Ng et al., 2021; Reid and Harley, 2021). Boulderfields and rockpools act as nursery grounds for many intertidal species (Raffaelli and Hawkins, 1996; Seabra et al., 2020) and as thermal refugia to the extremes experienced on open freely draining rock (Gunderson et al., 2019; Metaxas and Scheibling, 1993), yet both habitats will still be

subject to increasingly extreme temperatures as a result of ACC. For example, a study by Gunderson et al. (2019) looked at thermal variability beneath large rocks in intertidal boulderfields and found greater variability and higher maximum temperatures beneath high shore boulders compared to mid shore, regardless of either microhabitat receiving any direct solar influence.

Thermal tolerance studies of northeast Atlantic intertidal gastropods have mainly focussed on the responses of adult specimens, many of them taking place decades ago (see: Clarke et al., 2000; Evans, 1948; Sandison, 1967; Southward, 1958). We therefore wanted to explore how juveniles of intertidal gastropods local to southwest England, of different thermal affinities and vertical zonation, were physiologically responding to locally-experienced extreme temperatures. In two separate experiments exploring heatwave and cold spell tolerances, we compared the lethal and sub-lethal responses of Lusitanian (warm-temperate) and Boreal (cold-temperate) intertidal rocky shore gastropod species from southwest England to tide-out conditions, replicating both boulderfield (air) and rockpool (seawater) microhabitats. We simulated both seasonally ambient and extreme temperatures experienced separately in air and seawater (four treatments per experiment), as recorded using midshore Envlogger temperature loggers deployed locally in sun-exposed, shaded and rockpool rocky shore microhabitats since 2019. Four rocky shore gastropod species with differing thermal affinities were tested, additionally exploring ontogenetic differences in newly settled and year 1+ recruits for each species. The two warmer-water Lusitanian species (the trochids, *Phorcus lineatus* (da Costa, 1778) and *Steromphala umbilicalis* (da Costa, 1778)) and two colder-water Boreal species chosen (the littorinid, *Littorina littorea* (Linnaeus, 1758), and the trochid, *Steromphala cineraria* (Linnaeus, 1758)) have overlapping biogeographic ranges co-existing across different levels of the vertical shore gradient (Fig. 1). All species inhabit open bedrock, boulder and/or cobble fields on rocky shores as well as rockpools, with occupancy varying with season and life-stage. We tested the following hypotheses: (1) overall survivorship would be lower for new recruits than for year 1+ recruits; (2) survivorship for all species would be lowest in extreme air temperature treatments (heatwave/cold spell) replicating tide-out conditions in boulderfield habitats; (3a) extreme heatwave conditions would result in the lowest survivorship for Boreal (cold-temperate) species, whilst (3b) extreme cold spell conditions would result in the lowest survivorship for Lusitanian (warm-temperate) species; (4) induced inactivity (coma) would be highest for lowshore zoned species (*S. cineraria*); (5) recovery, where instances of inactivity have occurred, would be highest for highshore zoned species (*P. lineatus*).

2. Methods

2.1. Experiment setup

In order to identify newly recruiting (year 0+) and pre-maturation (year 1+) size, field surveys at Brixham Shoalstone (50.4013, -3.4960; 9th October 2021 and 2nd February 2022) and at Renney Rocks (50.3179, -4.1310; 10th October 2021 and 3rd February 2022) in south Devon, England, were conducted to measure the size structure of populations for each species classes (see Appendix 7.1). Species traits and size classes chosen for both experiments are shown in Appendix 7.2. Size classes for new recruits included basal diameters (shell height for *L. littorea*) (shown as heatwave /cold spell experiments) of *P. lineatus* = 4.0–6.0 mm/5.0–7.0 mm, *S. umbilicalis* = 3.0–5.0 mm/3.5–5.5 mm, *S. cineraria* = 3.0–5.0 mm/4.5–6.5 mm, *L. littorina* = 3.0–5.0 mm/4.0–6.0 mm. Year 1+ recruit size classes included basal diameters (shell height for *L. littorea*) (shown as heatwave/cold spell experiments) of *P. lineatus* = 10.5–12.5 mm/11.5–13.5 mm, *S. umbilicalis* = 6.0–8.0 mm/7.5–9.5 mm, *S. cineraria* = 6.0–8.0 mm/7.5–9.5 mm, *L. littorina* = 7.0–9.0 mm/8.0–10.0 mm. Trochid species had highest juvenile abundances on open bedrock (*P. lineatus* only), amongst low to high shore boulderfields, and in rockpools (*S. umbilicalis*, *S. cineraria*) at Renney

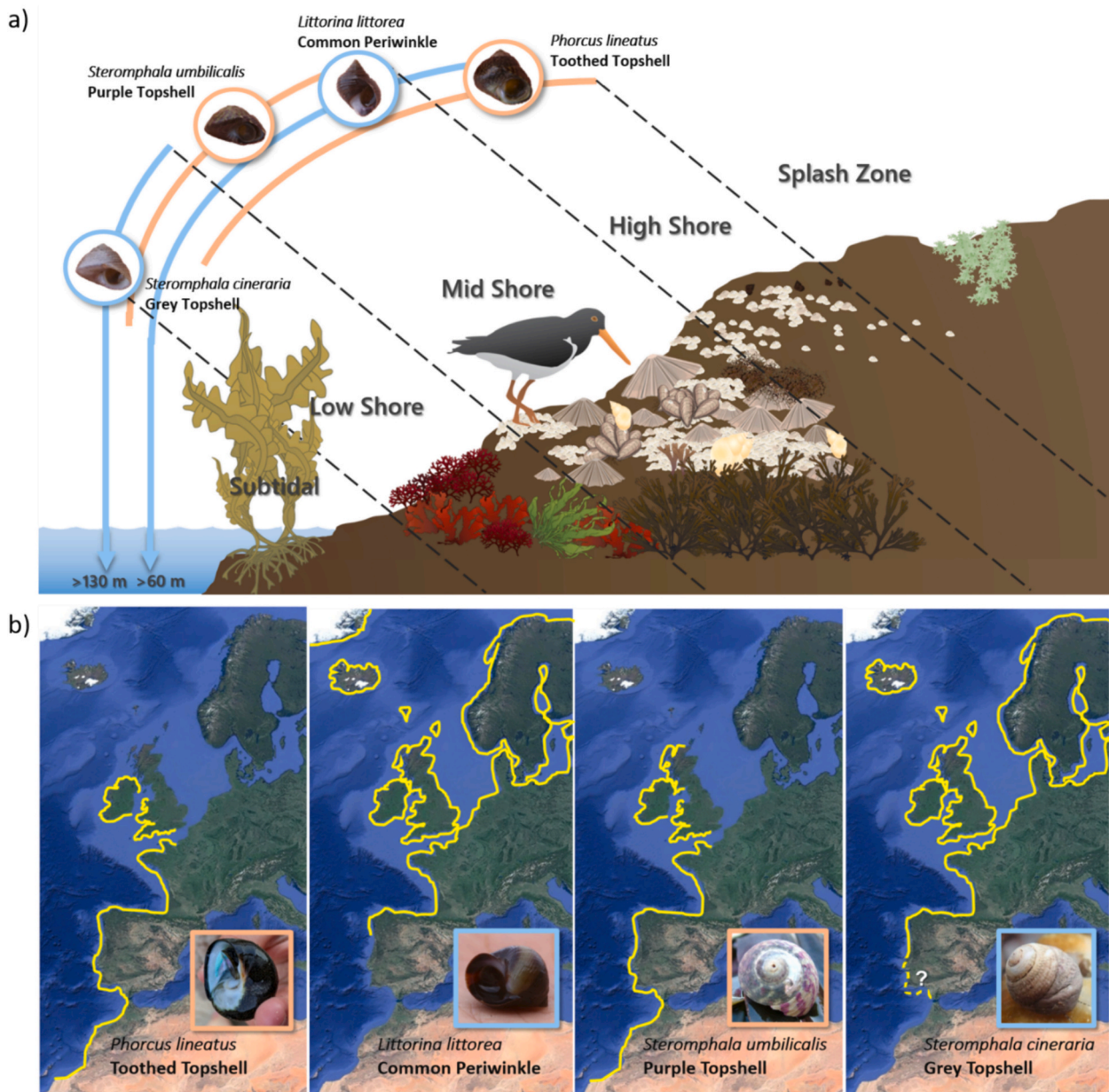


Fig. 1. a) Intertidal zonation and b) biogeographic ranges (yellow lines around coast) for all four study species, as identified from the literature. Thermal affinities are identified where photographs of Lusitanian (warm-temperate) species are outlined in orange/pink and Boreal (cold-temperate) species are outlined in blue. The southern biogeographic range limits in b) for *S. cineraria* are dashed with a question mark since intertidal individuals were not found during fieldwork carried out by the authors in 2019 (H. Parry-Wilson, pers. obs.), although subtidal habitats were not surveyed that the species may continue to inhabit. Faunal and algal illustrations in a) created by Jane Thomas and Tracey Saxby, Integration and Application Network, and Dieter Tracey, Department of Water Western Australia (ian.umces.edu/media-library). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Rocks. Juveniles of *Littorina littorea* were not found in high enough abundance at Renney Rocks, therefore this species alone was collected from boulderfields and rockpools at Brixham Shoalstone ~66 km eastwards. Following the field surveys, specimens were collected from Brixham Shoalstone (*L. littorea*) and Renney Rocks (*P. lineatus*, *S. umbilicalis*, *S. cineraria*) on 19th/20th of October 2021, and 1st/2nd March 2022 for the heatwave and cold spell thermal experiments respectively.

Individuals were acclimated to laboratory conditions in holding tanks with seawater temperatures set at 15 °C for the heatwave and 9.5 °C for the cold spell experiment over 5–6 and 3–4 days respectively, before being exposed to treatment conditions (see Appendix 7.3 for details on experimental setup and treatment conditions). Specimens within boulderfield (air temperature) treatments were additionally

exposed for six hours daily to ambient air temperatures during acclimation. *Littorina littorea* were acclimated for the maximum number of days for both experiments since specimen collection took place at Brixham Shoalstone a day earlier than trochid collections at Renney Rocks in both October 2021 and March 2022.

During acclimation, six individuals per species (*P. lineatus*, *L. littorea*, *S. umbilicalis*, *S. cineraria*) from each of the two size classes including new recruits (year 0) and year 1+ (maturing) recruits were allocated into five round 0.7 L (~15 cm diameter) replicate tanks per treatment, resulting in a total of 12 individuals per replicate tank, and 60 individuals per treatment per species (30 per size class); this setup remained for the duration of the main experiments. Each replicate tank had six circular mesh windows ~4 cm in diameter encouraging the flow of seawater or air depending on submersion/emersion, plus a larger

round mesh panel in the lid ~10 cm in diameter that additionally provided natural daylight to each of the tanks. Replicate tanks were cleaned daily during activity/mortality checks. Food was provided via small biofilm-covered pebbles every other day, collected from a nearby tidal estuary. All replicates received the same daily quantity of algae.

2.2. Experimental design

Two separate experiments were performed: a heatwave experiment was carried out between 25th October and 2nd November 2021, whilst a cold spell experiment was separately performed between 5th and 13th March 2022, both following periods of acclimation. During both experiments, no changes were made to the tank set-up identified previously (section 2.1). Aerial heatwaves in the British Isles and Ireland above 30 °C over the past two decades have been shown to persist for a maximum of nine days (Beckett and Sanderson, 2022). Nine days was therefore set as the duration for each of the separate heatwave and cold spell thermal experiments in this study to replicate future prolonged extreme temperature events.

The heatwave experiment in October 2021 tested physiological responses to extreme heat (increased) vs seasonally ambient temperatures both in both simulated boulderfields (air) and rockpools (seawater), and the cold spell experiment in March 2022 tested responses to extreme cold (decreased) vs seasonally ambient temperatures in both simulated boulderfields (air) and rockpools (seawater) (Fig. 2). Four thermal treatments within each separate experiment, totalling eight treatments overall, included (split into heatwave experiment/cold spell experiment temperatures): ambient air (15 °C / 9.5 °C), ambient seawater (15 °C / 9.5 °C), extreme increased/decreased air (40.0–43.0 °C / 1.5–2.5 °C), and extreme increased/decreased seawater (30.0 °C / 1.5–2.5 °C) (Fig. 3). Target temperatures were derived from temperature data recorded by midshore Envlogger temperature loggers (electricblue.eu) deployed at both Brixham Shoalstone, southeast Devon (50.4013, -3.4960) and Looe Hannafore, southeast Cornwall (50.3411, -4.4598) including extreme temperatures (Table 1) and seasonally ambient seawater temperatures (see Appendix 7.4). Seasonally ambient air temperatures were not set in a temperature-controlled room, but rather were predicted by previous years of EnvLogger data and determined by

natural outside air temperatures during each experiment, due to the exposed nature of the Marine Biological Association’s Seawater Hall.

All specimens were exposed to thermal treatments during a six-hour daytime tide-out event as experienced on shores in southern England. For the remaining 18 h each day, specimens were kept in locally and seasonally ambient seawater thermal conditions set at 15 °C for the heatwave experiment and 9.5 °C for the cold spell experiment to replicate tide-in conditions, therefore the experiment simulated a single daytime low-tide event within the spring tides of a lunar cycle as semi-diurnal tidal cycles could not be simulated with the available set-up (Fig. 3).

EnvLogger T2.4 temperature loggers (electricblue.eu) were used in each treatment to record air and seawater temperatures every 10–30 min from the beginning of acclimation to the end of each experiment. Technical issues resulted in the complete loss of ambient air temperature data for the heatwave experiment. EnvLogger air temperature data recorded at Looe Hannafore and Brixham Shoalstone two hours either side of low-tide (to ensure loggers were not immersed by seawater) were therefore used to infill the missing ambient air temperature data, recorded on the same dates of the experiment and only used if the data fell within the same experimental tide-out period (10:00–15:00 h, see Appendix 7.5 for temperatures experienced during each treatment for both experiments). This was considered sufficient since specimens in the ambient air temperature treatment were exposed to outside air conditions in the Marine Biological Association’s Seawater Hall.

2.3. Lethal and sub-lethal responses: survivorship, inactivity and recovery

All individuals were inspected for sub-lethal responses of inactivity or coma, or lethally for death immediately following daily exposure to each of the thermal treatments. Where individuals did not move nor respond to gentle external stimulus they were isolated, turned over so the aperture was facing upwards, and inspected over a ~ 60-min period. If no movement/response was observed during and after this time, specimens were placed in isolation overnight, recorded as inactive (experiencing coma) and a ‘spare’ individual of the same subsequent species and size class, clearly marked with epoxy paint on the shell, was placed into the respective replicate tank to maintain a constant density.

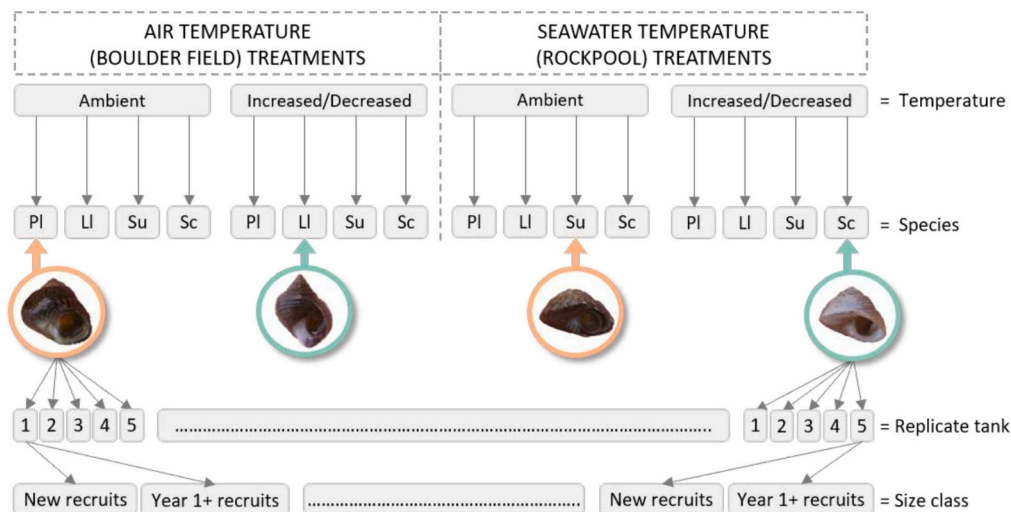
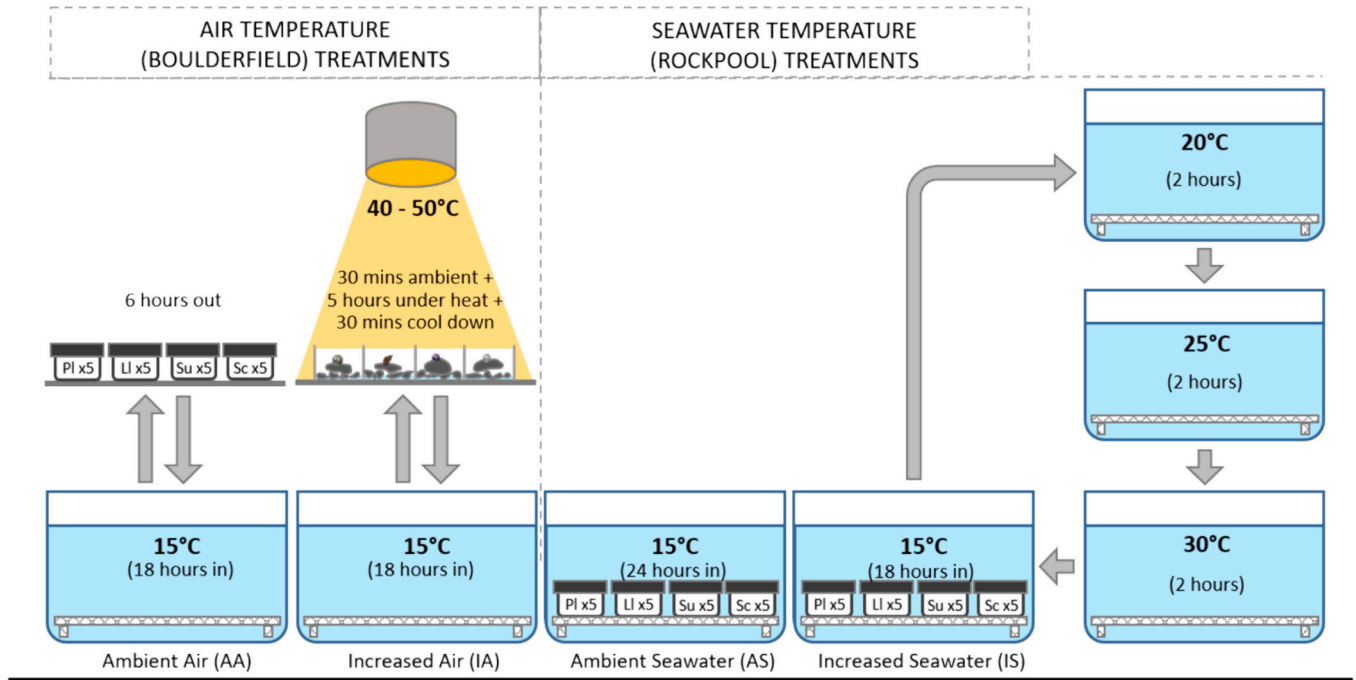


Fig. 2. Experimental design used for two temperature manipulation laboratory experiments: heatwave experiment (ambient, increased) carried out in October 2021 and cold spell experiment (ambient, decreased) carried out in March 2022. Four treatments per experiment were split across two microhabitat types, simulating seasonally ambient and extreme (increased = heatwave, decreased = cold spell) thermal conditions experienced in boulderfield (air) and rockpool (seawater) rocky shore microhabitats. Across both experiments there were therefore eight treatments in total as this design was replicated twice. Species included in the experimental design as shown above include: PI = *Phorcus lineatus*, LI = *Littorina littorea*, SU = *Steromphala umbilicalis*, SC = *Steromphala cineraria*. Species images shown in pink and blue circles show Lusitanian (warm-temperate) and Boreal (cold-temperate) thermal affinities respectively. Within each treatment, both size classes per species shared space in five replicate tanks per species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

A) Heatwave experiment: October 2021



B) Cold spell experiment: March 2022

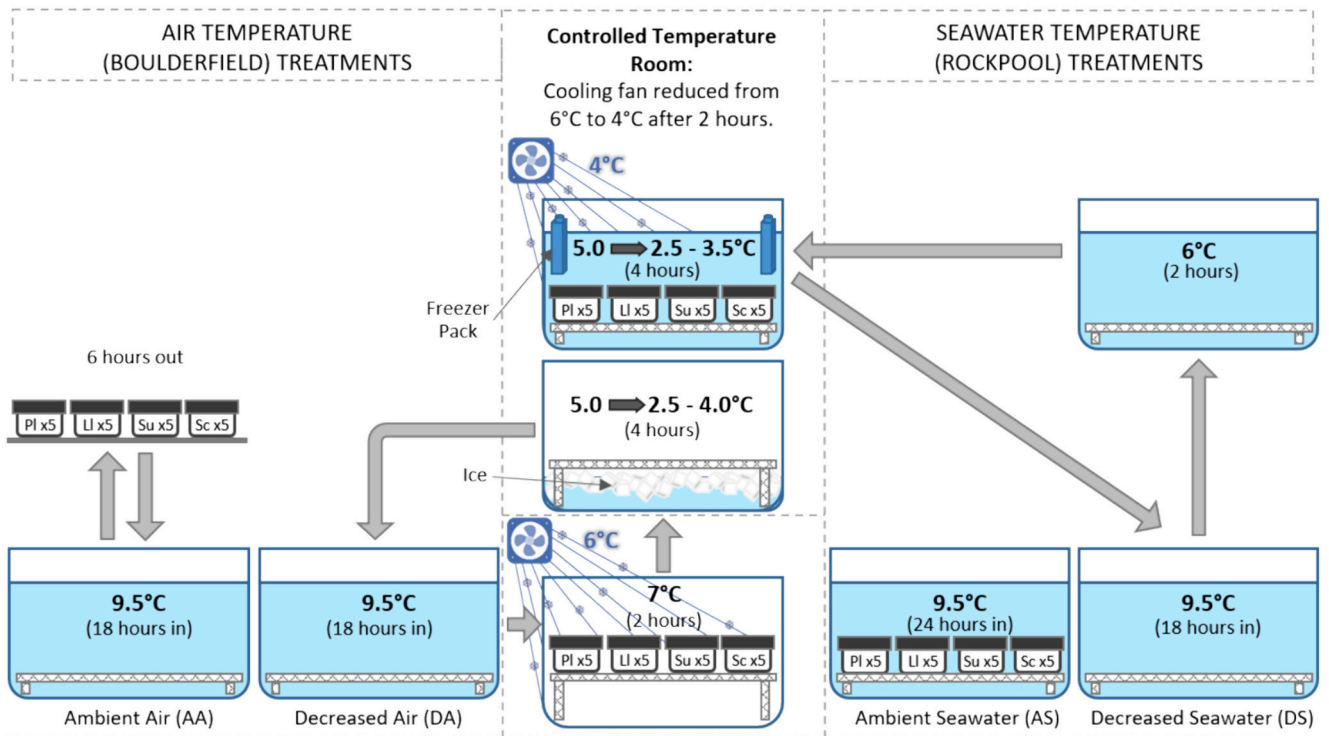


Fig. 3. Experimental design for both A) heatwave and B) cold spell experiments showing daily routine for all four thermal treatments per experiment, including extreme and ambient air (boulderfield) treatments and extreme and ambient seawater (rockpool) treatments. Both A) and B) show the timings of exposure to treatment conditions, with all treatments simulating a single daily six-hour tide-out event respective of seasonally ambient or extreme conditions, which were performed over a course of nine days per experiment. The four species within each treatment shown as small “x5” replicate tanks includes: Pl = *Phorcus lineatus*, Ll = *Littorina littorea*, Su = *Steromphala umbilicalis*, Sc = *Steromphala cineraria*. See Appendix 7.3 for further details on experimental conditions.

‘Spare’ individuals were held in a control tank from the beginning of acclimation, set to the same overnight holding tank temperatures according to thermal experiment. Individual animals from the experiment that had been isolated overnight due to inactivity were inspected the following morning before the experiment was continued. Any still not

attached to the substrate/tank, or demonstrating any movement, were recorded as dead. Isolated individuals demonstrating movement or attached to the isolation tanks were recorded as having recovered, then returned to their replicate tanks after removal of the marked ‘spare’ individual.

Table 1

Actual maximum and minimum tide-out temperatures recorded using EnvLog-ger temperature loggers (electricblue.eu) deployed in midshore (A) sun-exposed (tide-out air temperatures) and (B) rockpool (tide-out seawater temperatures) intertidal locations, both impacted by solar thermal influence during tide-out events in summer, and impacted by wind chill during tide-out events in winter. Loggers located at Brixham Shoalstone (50.4013, -3.4960) and Looe Hannafore (50.3411, -4.4598).

A) Sun-exposed loggers					
Year	Site	Maximum air temperature (°C) recorded	Date	Minimum air temperature (°C) recorded	Date
2019	Brixham	40.3	12/07/2019	-	-
	Looe	38.6	01/06/2019	-	-
2020	Brixham	40.0	02/06/2020	2.3	20/01/2020
	Looe	41.4	14/09/2020	2.5	30/03/2020
2021	Brixham	43.7	21/07/2021	1.3	08/03/2021
	Looe	43.3	21/07/2021	1.2	07/03/2021
B) Rockpool loggers					
Year	Site	Maximum seawater temperature (°C) recorded	Date	Minimum seawater temperature (°C) recorded	Date
2019	Brixham	28.2	02/07/2019	-	-
	Looe	30.4	04/07/2019	-	-
2020	Brixham	27.1	02/06/2020	4.5	20/01/2020
	Looe	29.5	24/06/2020	3.5	30/03/2020
2021	Brixham	28.3	21/07/2021	4.0	08/03/2021
	Looe	29.1	22/07/2022	2.5	07/03/2021

2.4. Data analysis

Mortality data for the heatwave thermal experiment were transformed into survivorship percentage per replicate tank (1:5) separately for boulderfield (air) and rockpool (seawater) set-ups, according to treatment (ambient, increased), species (*P. lineatus*, *S. umbilicalis*, *S. cineraria*, *L. littorea*) and size class (new recruits, year 1+ recruits). Following this, survivorship percentage data were arcsine-transformed, stretching out the upper and lower tails of the data when data are likely (and indeed were in this case) clustered around 100%. Due to small sample sizes and many 100% survivorship percentages recorded, assumptions of normality could not be met for parametric ANOVA regardless of transformations made, including log and square root, confirmed using Shapiro-Wilk's test ($p < 0.05$). Data were also found to be non-homogenous using Levene's test ($p < 0.05$). Therefore, non-parametric permutational three-way ANOVA tests were performed using the R 'vegan' package (Oksanen et al., 2022) on the arcsine-

transformed cumulative survivorship percentage data using Euclidean distance, between the three fixed factors (treatment, species, size class) and with replicate tank set as a random factor. Pairwise comparisons were performed for significant two-way interactions after subsetting by one factor to explore differences between the other, using Euclidean distance matrices and bonferroni adjustment.

Observational statistics were deemed sufficient to assess instances of inactivity that mainly occurred within the heatwave increased air temperature treatment, since daily inactivity occurrences per species were few to none.

3. Results

3.1. Inactivity and recovery

Only two instances of inactivity/coma were recorded in the cold spell thermal experiment: one in a *P. lineatus* new recruit in the ambient air temperature treatment on day 9 and the other for a *S. cineraria* year 1+ recruit in the same treatment on day 7 (Appendix 7.6). Both subsequently died.

The heatwave experiment induced the most inactivity or coma (Fig. 4), with the majority subsequently dying. Of 240 individuals per species (both size classes combined) within the heatwave experiment, more were rendered inactive in the increased air temperature treatment (*P. lineatus* = 2; *L. littorea* = 23; *S. umbilicalis* = 31; *S. cineraria* = 60), with only two inactive in the increased seawater (one each of *L. littorea* and *S. umbilicalis*) and one in ambient seawater (*S. cineraria*) treatments. Inactivity/coma in both the air (boulderfield) and seawater (rockpool) increased temperature treatments for the heatwave experiment increased with rank order from high to lowshore species: *Phorcus lineatus* (Fig. 4A) < *Littorina littorea* (Fig. 4B) < *Steromphala umbilicalis* (Fig. 4C) < *Steromphala cineraria* (Fig. 4D). Very few *P. lineatus* were rendered inactive during the heatwave experiment (0% in seawater, 3% in air; see Fig. 4A); as a consequence mortality was minimal. *Littorina littorea* showed maximum daily inactivity of 16% ($n = 5$) for new recruits on day 1 and 13% ($n = 4$) for year 1+ recruits after days 1 and 3 in the air increased temperature treatment respectively (Fig. 4B). In the increased seawater temperature treatment, only a single newly recruited *L. littorea* was inactive (3%). *S. teromphala umbilicalis* followed a similar pattern to *L. littorea* in the increased seawater temperature treatment, with a single (3%) year 1+ recruit being inactive. Conversely, higher *S. umbilicalis* daily inactivity maxima of 20% ($n = 6$) and 30% ($n = 9$) of new and year 1+ recruits respectively were observed in the increased air temperature treatment, occurring on day 3. Matching the lowest survivorship in both habitat types, 100% ($n = 30$) inactivity was recorded for both *S. cineraria* size classes after day 1 of heatwave increased air temperature conditions. This species is likely to be more sensitive as it is generally found immersed or on the damp undersides of boulders/cobbles. The highest daily percentage inactivity for any species in the increased seawater temperature treatment at 6% ($n = 2$) was also recorded for both new and year 1+ recruits of *S. cineraria* (Fig. 4D).

All instances of inactivity for *P. lineatus* and *S. cineraria* resulted in subsequent mortality. Of the inactive specimens, 25% of *L. littorea* and 6% of *S. umbilicalis* recovered and were returned to their respective heatwave treatments the following day; these were the only recoveries recorded in either the heatwave or cold spell experiment. The highest number of recoveries occurred after day 1 of increased air (boulderfield) temperature conditions, with three new and three year 1+ *L. littorea* recruits subsequently being returned to their respective replicate tanks on the morning of day 2. This higher frequency of recoveries is likely not representative of a response to treatment, but is simply a reflection of higher induced inactivity of *L. littorea* individuals on the first day of the experiment in the increased air temperature treatment, resulting in a larger proportion of recoveries. Individuals of *S. umbilicalis* exhibited two instances of recovery, with one new recruit recovering in the increased air temperature treatment after day 8 and one year 1+ recruit

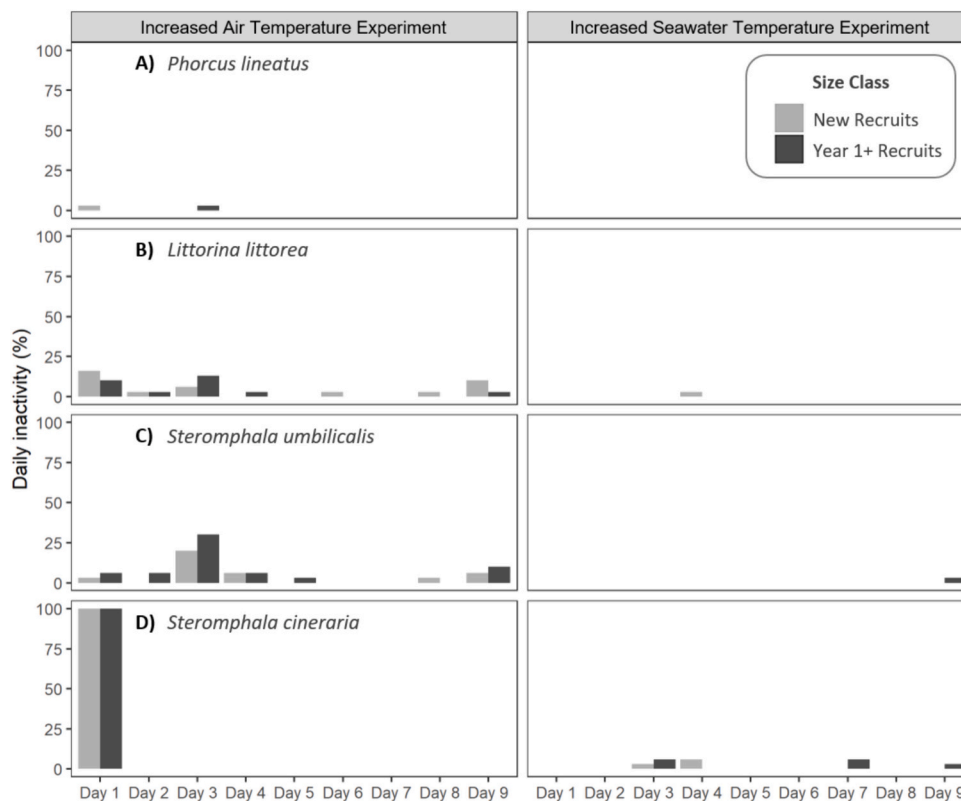


Fig. 4. Daily inactivity (%), shown only for increased air (boulderfield) and seawater (rockpool) temperature treatments, for new and year 1+ recruits during a nine-day extreme heatwave experiment run in October 2021. Results are separated by rocky intertidal species in order of zonation preference from high shore to low shore; (A) *Phorcus lineatus*, (B) *Littorina littorea*, (C) *Steromphala umbilicalis* and (D) *Steromphala cineraria*.

recovering after day 9 in the increased seawater temperature treatment.

3.2. Mortality

Mortality was highest for all species subject to the simulated heatwave increased air temperature treatment, followed by the heatwave increased seawater temperature treatment. A single mortality was recorded in ambient seawater conditions in the heatwave experiment (*S. cineraria*) and only two mortalities recorded during the entire cold snap experiment (*P. lineatus* and *S. cineraria*), therefore only extreme heatwave treatment survivorship data have been plotted in Fig. 5. The pattern of cumulative survivorship by the end of the experiment for simulated boulderfield habitats in aerial increased heatwave temperatures (Fig. 5A), followed the rank order of shore vertical zonation from high to low shore according to species (*P. lineatus* > *L. littorea* > *S. umbilicalis* > *S. cineraria*). For the heatwave increased seawater (rockpool) treatment (Fig. 5B), no mortalities were recorded for either Lusitanian (warm-temperate) species, *P. lineatus* and *S. umbilicalis*. For Boreal (cold-temperate) species in the heatwave increased seawater (rockpool) treatment, survivorship for *L. littorea* was greatest with a mean of 97% for new recruits and 100% for year 1+ recruits averaged across replicate tanks. For *S. cineraria*, means of 90% and 83% for new and year 1+ recruits respectively were recorded. These results suggest a slight sensitivity of premature Boreal species to heatwave temperatures in rockpools, with Lusitanian species unaffected.

Exploring the three-way interactions between the fixed factors of species (*P. lineatus*, *L. littorea*, *S. umbilicalis*, *S. cineraria*), treatment (ambient, increased) and size class (new recruits, year 1+ recruits) for cumulative survivorship in the heatwave experiment only, significant differences were found for the main effects of species and treatment separately when averaged across other factors, but not between size classes (Table 2). Only the two-way interactions between species and

treatment were significant for both air (boulderfield) and seawater (rockpool) treatments, reflecting differential survival. Neither of the three-way interactions were significant for air ($F_{(3,79)} = 1.181$, $p = 0.392$) or seawater ($F_{(3,79)} = 0.455$, $p = 0.741$) temperature treatments. Thus both new and year 1+ recruits displayed similar lethal responses to extreme air and seawater heatwave conditions for all species, with survivorship higher in ambient thermal treatments than increased temperatures. Pairwise comparisons of species identified that survivorship was significantly higher for *P. lineatus* specimens than all other species in the increased air (boulderfield) temperature treatment for the heatwave experiment; *L. littorea* and *S. umbilicalis* both had significantly higher survivorship than *S. cineraria* ($p < 0.01$) (Appendix 7.7). Extreme air temperatures had a significantly higher lethal effect on mid-low shore intertidal species of young trochids in a ranked order of vertical positioning of the species (see Fig. 5). Only *S. umbilicalis* demonstrated significantly higher survivorship than *S. cineraria* in the seawater (rockpool) increased temperature treatment ($p = 0.05$).

4. Discussion

4.1. Main findings

Understanding lethal and sub-lethal responses of phylogenetically similar ectothermic species of intertidal gastropods to the increasing number and intensity of climate-driven extreme temperature events will further our understanding of the wider impacts on rocky shore communities.

In this study we demonstrate that premature intertidal trochids do not appear to be more lethally thermally sensitive to extreme hot or cold conditions than adults for each respective species, although premature *L. littorea* may be slightly more lethally sensitive to heat. More frequent and unseasonable aerial heatwave events occurring for longer durations

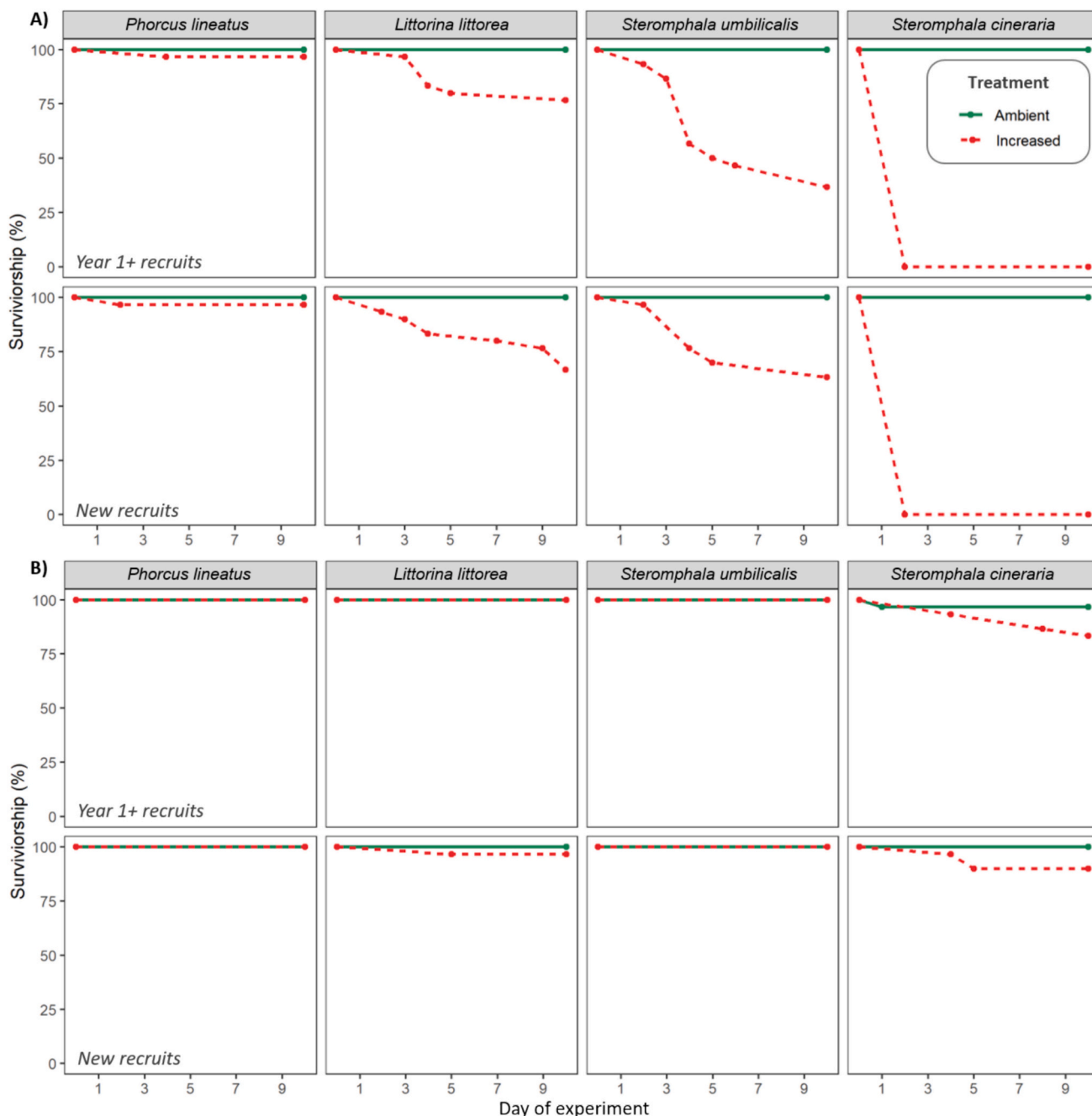


Fig. 5. Cumulative survivorship (%) across the nine-day heatwave experiment for (A) air (boulderfield) and (B) seawater (rockpool) temperature treatments run between 25th October (day 1) and 2nd November (day 9) 2021. Columns separate species and rows separate year 1+ (top) and new recruits (bottom). Point data show dates of recorded mortality.

are likely to detrimentally impact premature lowshore Boreal intertidal species, either through subtidal retreat, population declines, or local extinctions where thermal refugia are limited. This will subsequently impact recruitment to adult populations. Rockpools, where available, will provide essential thermal refugia for lowshore juveniles during aerial heatwave events, although mortalities of some Boreal species may occur within these submerged low tide habitats and will increase as aerial temperatures continue to rise.

Aerial cold spell events, simulated here using extreme cold temperatures currently experienced locally in southwest England, do not have appear to have any lethal or sub-lethal impacts on juvenile and maturing intertidal gastropods. This will facilitate the biogeographic extension of the leading range edge of warm-temperate species to higher latitudes,

promoting longer seasons of growth and reproduction. Instances of freezing conditions leading to mass mortalities as occurred in the extremely cold winter of 1962/1963 (Crisp, 1964) have rarely happened in recent decades.

Revisiting our hypotheses, overall survivorship was not found to be significantly different between new and year 1+ recruits for all species, and did not support hypothesis (1). Hypothesis (2) was partially supported, where the heatwave increased air temperature treatment resulted in the lowest survivorship, yet zero mortalities were recorded in the cold spell decreased air temperature treatment. Survivorship (relevant only to the heatwave experiment) was correlated with species shore zonation rather than species-specific thermal affinities (Boreal, Lusitanian) for the increased air temperature treatment, and did not provide

Table 2

Three-way permutational ANOVA results using Euclidean distance matrices exploring differences in arcsine-transformed cumulative survivorship percentages between species (*Phorcus lineatus*, *Littorina littorea*, *Steromphala umbilicalis* and *Steromphala cineraria*), size class (new recruits, year 1+ recruits) and treatment (ambient, increased) for the heatwave thermal experiment. Results were calculated separately for air (boulderfield) and seawater (rockpool) temperature treatments. SS = sum of squares and significant *p*-values are emboldened and cells highlighted grey.

	Df	Air temperature (boulderfield) treatments			Seawater temperature (rockpool) treatments		
		SS	F.Model	P-value	SS	F.Model	P-value
Species	3	5.854	42.502	0.001	0.388	9.998	0.001
Size class	1	0.010	0.220	0.642	0.009	0.683	0.444
Treatment	1	11.211	244.178	0.001	0.106	8.193	0.003
Species:Size class	3	0.163	1.181	0.342	0.080	2.049	0.113
Species:Treatment	3	5.854	42.502	0.001	0.213	5.494	0.002
Size class:Treatment	1	0.010	0.220	0.645	0.000	0.000	1.000
Species:Size class:Treatment	3	0.163	1.181	0.392	0.018	0.455	0.741

support for hypotheses (3a) and (3b). There was evidence to support hypothesis (4) as the highest overall inactivity was recorded for low shore species, *S. cineraria*, in both the heatwave increased seawater and increased air temperature treatments: the latter treatment resulted in full mortality of all subjected specimens after a single day. Recovery was only recorded for *L. littorea* and *S. umbilicalis*, thus partially supporting hypothesis (5) since inactivity was highest for *L. littorea*, a high-midshore species, yet inactivity resulted in mortality for high-shore species *P. lineatus*. In general, inactivity led to subsequent mortality with few instances of recovery, mostly in *L. littorea* and to a lesser extent *S. umbilicalis*.

4.2. Extreme heat restructuring intertidal communities in a warming world

Critical thermal maxima in ectotherms can vary depending on the rate of heating, generally resulting in higher temperature tolerances with more gradual exposure (Evans, 1948; Rees, 1941). Upper thermal tolerances can also vary with the location of individuals along the biogeographic distribution of a species (Kuo and Sanford, 2009; Zippay and Hofmann, 2010) as shown by *L. littorea*, which has demonstrated higher heat tolerances at lower latitudes (Sandison, 1967). Lethal thermal limits have previously been estimated at 45.0–45.8 °C for *P. lineatus*, 46.0 °C for *L. littorea*, 41.8–42.1 °C for *S. umbilicalis*, and 35.5–36.2 °C for *S. cineraria*. These are based on specimens collected from Cardigan Bay, Wales (Evans, 1948) and southwest England (Southward, 1958), although these studies only included adult specimens and lethal limits that were determined in seawater and not aerial temperatures.

Both thermal and desiccation tolerances have been proposed to set upper intertidal zonation limits (Connell, 1972; Foster, 1971; Wolcott, 1973). For rocky shore gastropods, desiccation tolerances (recorded as rates of water loss) have been shown to increase with increasing organismal shore height (Davies, 1969). In contrast, temperature tolerances have actually been shown to increase as a function of vertical zonation range (Stickle et al., 2017). This experiment indicates that juveniles of the highest shore species, *P. lineatus*, demonstrated the highest tolerances against extreme thermal stress, suggesting similar thermal sensitivities as adults. This is despite both *L. littorea* and *S. umbilicalis* having wider vertical zonations than *P. lineatus* (see Fig. 1a), inhabiting a greater variety of microhabitats on rocky shores, having broader

latitudinal ranges, and demonstrating instances of recovery after experiencing heat-coma. Increased heatwave air temperature-induced mortalities of *L. littorea* (Fig. 5a) suggest that premature specimens are more thermally sensitive than adults, as temperatures in this treatment (up to 42.9 °C) were 3.1 °C less than adult lethal thermal limits (Evans, 1948; Southward, 1958).

Steromphala umbilicalis is a warm-temperate generalist species (Wort et al., 2019) that occupies multiple microhabitats throughout its broad range. Some individuals died in simulated extreme heatwave temperatures up to 42.9 °C, reflecting the lethal heat limits of adults at 41.8–42.1 °C (Evans, 1948; Southward, 1958) and suggesting that premature specimens of *S. umbilicalis* may have similar thermal sensitivities to adults. This species has demonstrated relatively rapid extensions of the leading range edges along the northern Scottish and southern English Channel coasts over recent decades that positively correlate with rising sea surface temperatures (Kendall and Lewis, 1986; Mieszkowska et al., 2006). *Steromphala umbilicalis* also exhibits protracted spawning events across the year for populations in mid-range to southern biogeographic limits (Bode et al., 1986; N. Mieszkowska, unpublished data). This suggests that increasing seawater temperatures and milder winters as a result of ACC may benefit northern range-edge populations of *S. umbilicalis*, if thermal conditions gradually alter to those currently experienced by mid-southern biogeographic range of the species and thermal refugia are available during aerial heatwave events. There is certainly no current sign of detrimental effects of low temperatures during cold spells.

Survivorship was lowest in the heatwave increased air temperature treatment, causing deaths of the lowest shore species, *S. cineraria* after only one day of exposure in simulated boulderfield habitats. The upper lethal (35.5–36.2 °C) temperature limits of the species (Evans, 1948; Southward, 1958) are lower than exposure temperatures in the heatwave air temperature treatment. Although *S. cineraria* is a lowshore to subtidal species usually found immersed in water, in standing water, or in damp places amongst pebbles/boulders on the lowest tides, field studies of *S. cineraria* abundances in southwest England have occasionally found specimens located under mid-lowshore boulder and cobble habitats at some study sites (H. Parry-Wilson, pers. obs.) outside of the peak summer season. In natural systems, mobile gastropods often demonstrate seasonal migration up and down the vertical gradient of intertidal shores (Markowitz, 1980; Williams, 1965; Underwood, 1973). *S. cineraria* retreats lower down the shore and/or subtidally

during summer months (Micallef, 1969; Underwood, 1973), as well as into microhabitat refuges including under stones and/or in shallow pools. High air temperature events could therefore cause mass mortalities in thermally sensitive mobile species if they were to occur unseasonably, especially since the critical thermal maxima of species can vary according to season (Evans, 1948). Behavioural adaptation, however, is not always going to be possible for species without any option of thermal refugia or vertical zonation retreat, therefore forcing them to either physiologically adapt or die.

Very few laboratory studies have explored lethal limits in air for intertidal species (although see: Jones et al., 2009; Leung et al., 2019; Schneider, 2008). Building on these experiments, a multi-stressor approach testing both thermal and desiccation tolerances to heat stress would therefore generate data to assist with further understanding of the lethal limits for each species in increasingly extreme aerial heatwave events, on top of persistently rising air and sea surface temperatures from pervasive ACC. Furthermore, testing sub-lethal responses of both premature and fully mature specimens to heat stress, such as analysing heat stress impacts on spawning, larval development and growth, would assist in the understanding of how rising temperatures and extreme events may impact population success into the future.

4.3. Cold resilience

Almost no instances of juvenile mortality or inactivity for these intertidal species were recorded in the cold spell experiment, echoing previous studies showing that adults are capable of surviving air temperatures well below 0 °C and have freezing resistances (Murphy, 1983; Theede, 1973). Adult *L. littorea*, for example, have been shown to survive at extreme cold air temperatures down to −13 °C (Murphy, 1979). The littorinid species, *Littorina scutulata* (Gould, 1849), move to sheltered microhabitats such as crevices, under boulders or seaweed canopies when exposed to extreme winter cold temperatures (Reid and Harley, 2021). This is a behaviour that has similarly been observed for *S. umbilicalis* specimens in southwest England and northern France (H. Parry-Wilson, pers. obs.) that became more abundant in rockpools during low tide in colder months. Of the three trochid species within this study (*P. lineatus*, *S. umbilicalis*, *S. cineraria*), lower thermal tolerance limits have also been shown to be related to upper vertical shore zonation, with higher shore species more tolerant of cold temperatures than those inhabiting the lower shore (Southward, 1958). As with upper lethal limits, lower thermal tolerance experiments are currently limited to the study of adult specimens, although freezing resistance in intertidal barnacles has shown that earlier life stages were less cold-tolerant than adults (Theede, 1973). Although extreme cold spell events are likely to decrease in frequency with the continuation of ACC (Begum et al., 2022; Diffenbaugh et al., 2005; Meccia et al., 2024), when these events do occur they appear to be intensifying (Herring et al., 2021; Yin and Zhao, 2021). For rocky shore species, extreme winter temperatures have previously resulted in extensive and complete mortalities of populations of both Lusitanian species, *P. lineatus* and *S. umbilicalis*, along a substantial length of British shoreline (Crisp, 1964). Further investigation of the lethal responses of early life stages of rocky shore organisms to extreme cold temperatures and/or freezing would broaden our understanding of how cold shock impacts intertidal communities, with species differentially and phenotypically adapting to rising aerial and seawater temperatures in increasingly milder thermal conditions in southern Britain.

4.4. Study limitations

Differences in the acclimation times for both heatwave (5–6 days) and cold spell (3–4 days) experiments were unfortunately unavoidable as a result of combined COVID-related restrictions, laboratory availability, and tidal regimes required for specimen collection. Comparisons of heatwave versus cold spell experiment results were therefore not formally statistically compared. Given the lower induction of inactivity

and subsequent mortality in the cold spell experiments, the acclimation period was clearly sufficient.

Although the heatwave experiment was originally planned for August 2021 when annual summer British heatwaves (aerial and marine) have been most frequent between June and September (Mccarthy et al., 2019; Mieszkowska et al., 2021; Simon et al., 2023), COVID-related equipment issues postponed the experiment by two months until October 2021. This provided an opportunity to measure lethal responses of all four species within the extending annual seasonal range for heatwave events up to November (Mccarthy et al., 2019; Mieszkowska et al., 2021; Tinker et al., 2020).

The experimental protocol in this study did not allow movement away from thermal stress into other microhabitat types, therefore preventing natural buffering behaviours (Ng et al., 2017) for specimens seeking thermal refugia. That being said, pebbles were provided within each of the 'boulderfield' (air) treatments to replicate some natural refugia from direct thermal influence of the basking lamps (heatwave experiment) and cooling fans (cold spell experiment), along with <1 cm of seawater at the bottom of each tank in both experiments. Intertidal rocky shore gastropods show explorative behaviours in an attempt to find suitable macro- and microhabitats to use as refuges during thermally stressful events (Moisez et al., 2020), especially where the requirement of thermal refugia becomes more critical towards range edges when thermal tolerance limits of a species are reached (Lima et al., 2016). For example, towards southern range limits of the cold-temperate patellid species *Patella vulgata* (Linnaeus, 1758), shaded rock surfaces are used as thermal refugia from exposure to intense solar radiation (Lima et al., 2016), as well as barnacle-covered solar-exposed bedrock that drives down temperatures compared to bare rock surfaces (Moisez et al., 2020). The availability of thermal refugia, however, depends on the geomorphology and biological communities of rocky intertidal shores (Lima et al., 2016). Although the lower limits of vertical shore zonation have been shown to be driven by biological interactions such as predation and/or competition (Connell, 1961), the two Boreal species within this experiment, *L. littorea* and *S. cineraria*, can both occur sublittorally, giving them the opportunity to vertically retreat from thermal extremes where intertidal refugia are not available. Both Lusitanian species tested in this experiment, *P. lineatus* and *S. umbilicalis*, only inhabit the intertidal zone, with no subtidal inhabitation throughout their biogeographic range. During a displacement study to shallow subtidal waters, *S. umbilicalis* specimens returned promptly to the intertidal (Thain et al., 1985). Increasing aerial heatwave temperatures in northwest Africa (Iyakaremye et al., 2021; Iyakaremye et al., 2022) towards the southern biogeographic limits of both Lusitanian species could soon cause range contractions if intertidal topographical complexity is also low, due to a lack of thermal refugia (Lima et al., 2016). The limitation of movement of individuals within this study could therefore be considered reflective of minimal/no availability of thermal refugia, where most premature individuals of Lusitanian species would survive in conditions tested in this experiment, but potentially not in future aerial heatwave temperatures.

5. Conclusion

Although winter cold spell events are on the decrease in northern Europe, extreme heatwave events are increasing in frequency, duration and intensity, impacting both aerial and seawater temperatures and occurring increasingly across a broader seasonal duration annually. Premature intertidal trochid species tested here do not appear to be more lethally sensitive to thermal extremes to those of adults, although *L. littorina* may be more lethally sensitive than adults to heat. Extreme cold spell conditions do not appear to negatively impact survival of juvenile intertidal gastropods, enabling the spread of warm-temperate species. Extreme aerial heatwave conditions are likely to have increasingly devastating impacts on the survival of lowshore Boreal species, especially sessile or sedentary species that cannot relocate to and/or

utilise thermal refugia. Further research on lethal and sub-lethal effects of aerial and marine heatwaves on intertidal species of various life stages should be conducted as summer temperatures continue to increase. This research would further our understanding of the wider implications on intertidal communities, especially where polewards range shifts are limited by habitat gaps, creating localised species extinctions.

CRedit authorship contribution statement

H.M. Parry-Wilson: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **P.B. Fenberg:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Conceptualization. **S.J. Hawkins:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Conceptualization. **N. Mieszowska:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Hannah Parry-Wilson reports financial support was provided by Natural Environment Research Council. If there are other authors, they declare

that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

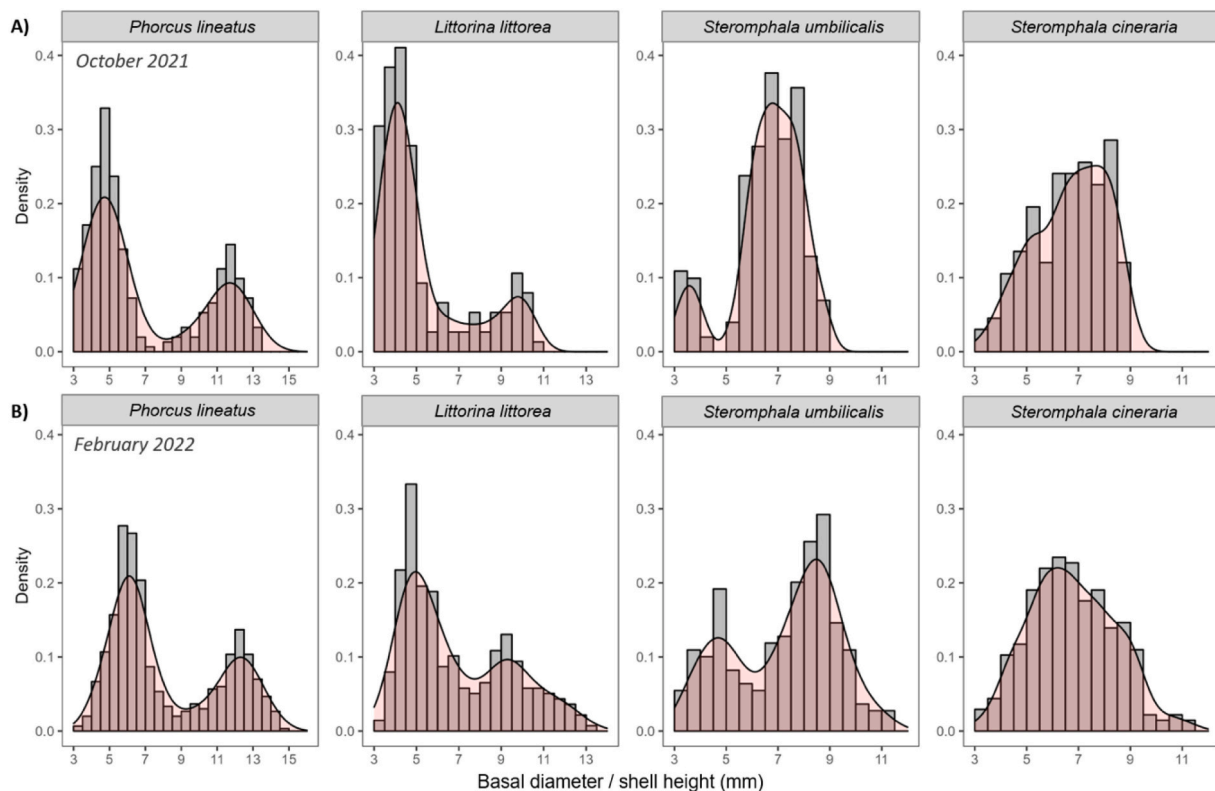
Data will be made available on request.

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Appendix A. Appendices

A.1. Field survey species size-densities



Appendix 7.1. Sample population densities (0–1) to determine size classes for new and year 1+ recruits, both for the (A) heatwave and (B) cold spell thermal experiments. Species were measured during field surveys on (A) 8th and 9th October 2021 and on (B) 2nd and 3rd February 2022 at both Brixham Shoalstone (50.4013, –3.4960) and Renny Rocks (50.3179, –4.1310) in south Devon. *Littorina littorea* size-densities shown for Brixham Shoalstone, with the three trochid species (*Phorcus lineatus*, *Steromphala umbilicalis*, *Steromphala cineraria*) all shown for Renny Rocks. Minimum size was restricted to 3 mm basal diameter / shell height (mm) to ensure specimens could be inspected by eye for inactivity/mortality during the lab experiment. Overlaying kernel density estimate visually highlighting peaks in population density. Note the differences in size range along each x-axis per species, which is varied due to the different sizes of maturation that was a target upper size limit for October surveys (Table 1).

A.2. Species life history traits and collection sizes

Table 7.2

Life history traits and selected specimen collection sizes for each of the heatwave (October 2021) and cold spell (February/March 2022) thermal experiments, according to size classes including new and year 1+ recruits.

Species	Biogeographic Range	Preferred shore exposure	Preferred vertical gradient	Micro-habitat preference		Size & age at maturation (mm)	October 2021		February 2022	
				Juvenile	Adult		New recruits size class (mm)	Year 1+ recruits size class (mm)	New recruits size class (mm)	Year 1+ recruits size class (mm)
<i>Phorcus lineatus</i>	Northern Welsh coast (Mieszkowska et al., 2007; Mieszkowska, 2022) to Morocco (Crothers, 2001).	Moderately exposed shores (Mieszkowska et al., 2007).	Mean high water neaps to mean low water neaps (Evans, 1947).	Cryptic habitats (Crothers, 2001); in pools, under stones and in crevices (Fretter and Graham Fretter and Graham, 1977).	Fairly sheltered level rock, areas of boulders and shingle, sheltered gullies (Evans, 1947).	Shell width 18 mm (Fretter and Graham Fretter and Graham, 1977; Underwood, 1971) at ~2 years of age (Desai, 1966)	4.0 – 6.0	10.5–12.5	5.0 – 7.0	11.5–13.5
<i>Steromphala umbilicalis</i>	Northern Scottish coast (Lewis et al., 1982; Mieszkowska et al., 2007) to Morocco/northwest Africa (Fretter and Graham Fretter and Graham, 1977; Lewis, 1986; Southward et al., 1995)	Very exposed to very sheltered shores (Evans, 1947).	Mean high water neaps to mean low water neaps (Mieszkowska Diffenbaugh et al., 2005), sometimes as low as mean low water springs (Evans, 1947).	Pools and crevices as well as flat, fairly sheltered rocks, boulders and stones, more commonly associated with fucooids (Evans, 1947).	Pools and crevices as well as flat, fairly sheltered rocks, boulders and stones, more commonly associated with fucooids (Evans, 1947).	Shell width 8–9 mm at ~18 months (Williams, 1964a)	3.0 – 5.0	6.0 – 8.0	3.5 – 5.5	7.5 – 9.5
<i>Steromphala cineraria</i>	North Norway & Iceland to Gibraltar (Fretter and Graham Fretter and Graham, 1977), although no intertidal specimens found on mid-southern Portuguese coasts in 2019 (H.Parry-Wilson, pers. obs.)	Very exposed to very sheltered shores (Evans, 1947)	Below mean low water neaps (Crothers, 2001; Evans, 1947)	Under boulders & ledges, in crevices, pools, on rocky shores with some sand, amongst light algae (Fretter and Graham Fretter and Graham, 1977).	Under boulders & ledges, in crevices, pools, on rocky shores with some sand, amongst light algae (Fretter and Graham Fretter and Graham, 1977). Mainly subtidal amongst kelp (H.Parry-Wilson, pers. obs.).	Shell width 8 mm in 2nd year (Underwood, 1971)	3.0 – 5.0	6.0 – 8.0	4.5 – 6.5	7.5 – 9.5
<i>Littorina littorea</i>	White Sea, Russia to northern Portugal (Bequaert, 1943).	Semi-exposed to very sheltered shores (Evans, 1947; Fretter et al., 1980). Also tolerant of brackish waters (Jaeckel, 1952).	Mean high water neaps/springs to mean low water springs (Evans, 1947). Also sublittorally to 60 m, especially in northern range (Fretter et al., 1980).	Intertidal cracks and amongst barnacles (Fretter et al., 1980). Some debate to subtidal settlement (Daguzan, 1976; Smith and Newell Smith and Newell, 1955)	Sheltered gullies (Evans, 1947), pools, under boulders and/or algae on rocky shores (Fretter et al., 1980). Also occur on wet mud, sometimes sand with some solid substratum (Fretter et al., 1980).	Between 11 and 18 months at 11–12 mm shell height (Daguzan, 1976; Fish, 1972; Guyomarc’h-Cousin, 1975; Tattersall, 1920; Williams, 1964b).	3.0 – 5.0	7.0 – 9.0	4.0 – 6.0	8.0–10.0

A.3. Experimental conditions

Specimens were acclimated in isolated 1000 L tanks of natural seawater pumped directly into the Marine Biological Association aquarium system from Plymouth Sound within the main seawater hall. Tanks were positioned under ceiling windows to allow for natural daylight and with a permanently consistent flow of external fresh air, to provide ambient air to the relevant (boulderfield) treatments. Acclimation tanks were then used for the duration of the experiment as overnight holding tanks, simulating locally ambient seawater temperatures during tide-in events. Holding tank ambient seawater temperatures were set to 15 °C for the heatwave and 9.5 °C for the cold spell experiment, rounded up from mean high tide daytime seawater temperatures for October and early March recorded by midshore EnvLogger temperature loggers at both Brixham Shoalstone and Looe Hannafore since 2019 (Appendix 7.4). Tank seawater temperatures were monitored constantly using a GHL temp digital probe and controlled using D—D titanium 650w water heaters and TECO 2000 water chillers that automatically adjusted holding tank seawater temperatures if they decreased/increased by ± 1 °C. Seawater temperatures and salinities were monitored for all holding tanks on a daily basis using a YSI Professional Plus probe. Any salinities found to exceed 35 ppt were added to with fresh water until the salinities dropped below 34.5 ppt.

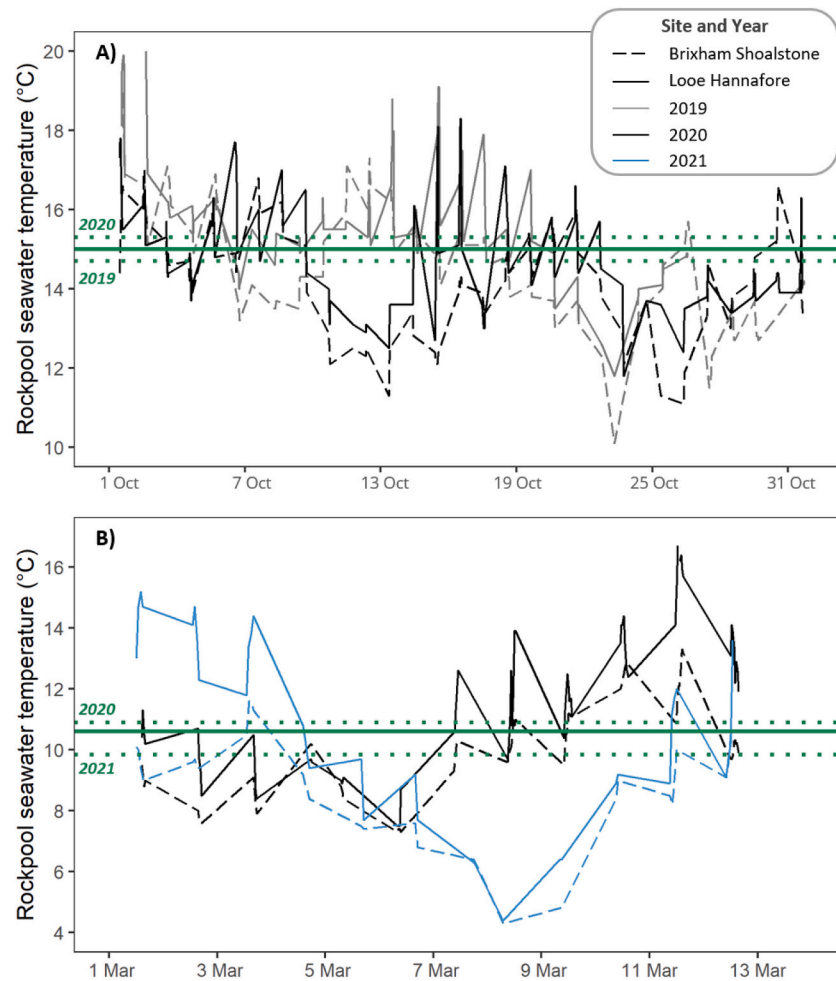
During acclimation, specimens in ambient, increased, and decreased air temperature (boulderfield) treatments were removed from submersion in their respective treatment tanks and exposed to ambient air temperatures for six hours daily to replicate a daily tide-out event. Specimens in simulated rockpool habitats were kept constantly submerged to replicate natural rockpool conditions. The hours chosen for daily tide-out events (09:30–15:30) did not precisely replicate locally low tide times for each day of the experiment, although were chosen as they closely follow tidal cycles during daylight hours in south Devon. Dual tide-out events, replicating natural intertidal conditions in southwest England, were not possible for this study.

A.3.1. Simulated ambient conditions

Specimens in the ambient seawater temperature (rockpool) treatments were submerged for the full duration of each nine-day experiment. Although the ambient seawater treatment tanks were set at fixed temperatures, natural tide-out conditions for rockpools were still simulated with this set-up. The tanks were subject to some temperature fluctuation from outside air temperature influence within the Marine Biological Association's main seawater hall, in addition to fluctuations from the water heaters and chillers. Although rockpools in natural systems fluctuate in seawater temperature to higher ranges during tide-out events in natural systems as a result of solar and weather influences (Appendix Fig. 7.3.1a), these were not directly replicable within the laboratory system. Adjustments to overnight holding tank temperatures were not deemed necessary, since locally ambient tide-out rockpool mean temperatures were found to be within 1.1 °C of locally and seasonally ambient seawater (tide-in) temperatures as recorded by EnvLoggers (Appendix 7.4). Specimens in the ambient seawater temperature (rockpool) treatment only experienced emersion from seawater for inspection for inactivity/mortality, feeding and cleaning.

Specimens in the ambient air temperature (boulderfield) treatments were submerged in holding tanks overnight simulating locally ambient seawater temperatures, and were exposed to ambient air temperatures within the main seawater hall of the Marine Biological Association for six hours daily to replicate a single tide-out event.

A single EnvLogger temperature logger was placed into each overnight holding tank, recording seawater temperatures every 30 minutes from the first day of acclimation until the end of each nine-day experiment to provide a constant record of seawater temperatures for each treatment. One EnvLogger temperature logger, also recording every 30 minutes, was placed directly above the overnight holding tanks in the Marine Biological Association's seawater hall to record ambient air temperatures.



Appendix Fig. 7.3.1a. Daytime rockpool temperatures recorded during low tide events, where data is shown for a 1–2 h period either side of each low tide event dependent on tidal height. Data were recorded by Envlogger temperature loggers (electricblue.eu) every 30 min in the months of (A) October and (B) during the first 10 days of March. EnvLoggers were deployed midshore within shallow coralline intertidal rockpools at both Brixham Shoalstone, South Devon (50.4013, –3.4960), and Looe Hannafore, South Cornwall (50.3411, –4.4598). Legend on plot (A) identifies linetypes according to site and year of temperature data for both plots. Linetype (longdash, solid) identifies site and line colour identifies year. Dotted green horizontal lines show mean rockpool seawater temperature per year (labelled on left of plot), whilst solid green lines identify mean of all temperature data per plot.

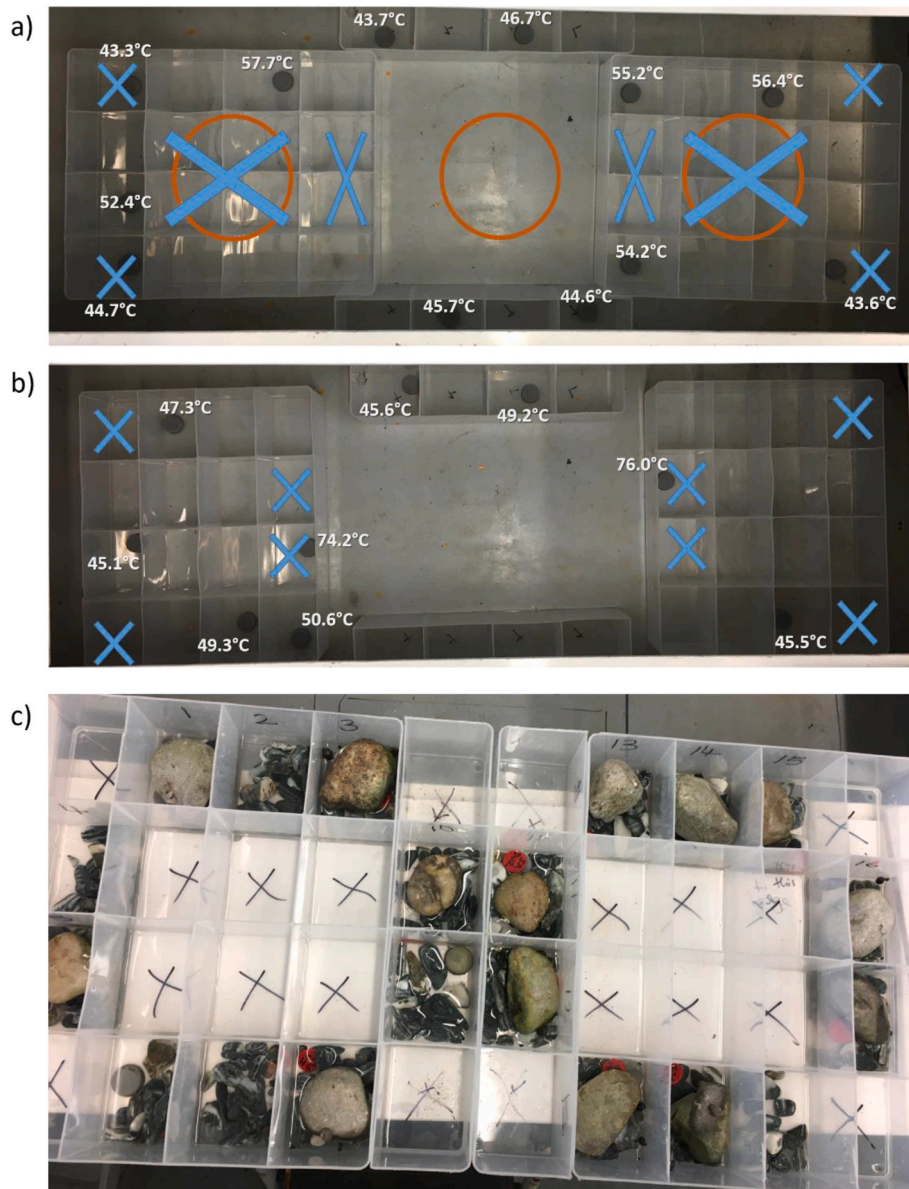
A.3.2. Simulated heatwave conditions

Maximum tide-out temperatures under solar radiation, taken from EnvLogger temperature loggers deployed on midshore rocky intertidal exposed bedrock and in rockpools at both Brixham Shoalstone and Looe Hannafore, were used as target air (43.7 °C) and seawater temperatures (30.4 °C) for increased heatwave treatments in this experiment (Table 1).

Specimens in the increased air temperature (boulderfield) treatment were removed from their submerged overnight holding tanks every morning and placed into plastic trays with numbered sections, allowing a 30+ minute resting period before being placed under heated reptile basking lamps (Appendix Fig. 7.3.2). Each section of the plastic trays had previously been tested during pilot studies for maximum daily air temperatures using a high range dimmer thermostat (Habistat; 40–600 watts) to separately adjust two basking lamps to between 24 °C and 40 °C. As only 15 EnvLoggers were available to test the temperatures within each of the 40 tray sections, each of the sections were tested systematically and 20 sections were approved for use in the experiment where maximum temperatures within pebbles recorded 40–50 °C (Appendix Fig. 7.3.2), chosen as a suitable temperature range for this study due to the maximum heatwave temperatures recorded by locally deployed exposed EnvLogger temperature loggers (Table 1). To replicate a rocky shore pebble/cobble field, aquarium gravel slate pieces covered the bottom of each plastic tray section with ~0.7–1.0 cm of seawater to replicate underlying water in a pebble/boulderfield, plus a single pebble of 5–7 cm diameter/length to provide some natural refuge from the direct heat source, since warming generally drives sheltering behaviour (Leung et al., 2019). Specimens from each replicate tank were placed into a different numbered section each day, chosen at random to ensure variability in the maximum temperatures experienced within the range of temperatures recorded throughout the tray sections. This design was set to mimic the natural variability of temperatures experienced in rocky shore boulderfields that are mobile microhabitats, with rocky gastropods also relatively mobile by nature. Eight Envlogger thermal loggers were also placed into the same allocated numbered sections on a daily basis to record any variations in temperature experienced daily under the heat of the reptile basking lamps.

Reptile basking lamps were turned on at 10:00 daily and switched off again at 15:00. Although removed from overnight holding tanks for a six-hour tide-out event on a daily basis, a five-hour time period was chosen for exposure to the reptile basking lamps (as extreme hot air temperature conditions) to firstly allow the lamps to heat up fully, before reaching their hottest temperatures across the naturally hottest hours of the day (11:00–15:00; metoffice.gov.uk) during heatwave events. Following extreme temperature exposure, specimens were left for 20–30 min in ambient air temperature, before being returned to their respective replicates tanks and submerged into their 1000 L overnight holding tank to replicate an

incoming tide. After ~30 min of submersion, specimens were then removed, inspected for inactivity/mortality, algal-covered pebbles replaced and replicate tanks cleaned, then again returned to the overnight holding tanks until the following day.



Appendix Fig. 7.3.2. Evolution of pilot study method to determine temperatures of tray sections positioned beneath reptile basking lamps as part of the heatwave increased air temperature treatment. Photographs taken on a) 4th August 2021, b) 19th August 2021 and c) 28th October 2021. Image a) shows set positions of three overhead basking lamps (orange circles) that were dropped down through holes in a plastic tank lid during each pilot (and subsequently during the experiment) to best maintain heated temperatures. Both a) and b) show maximum temperatures recorded by EnvLogger temperature loggers (electricblue.eu) recording data every 10 min during pilot studies. Image c) shows final tray setup with 20 from 40 selected sections (crosses identify rejected sections), complete with gravel and large pebble 'boulderfield' habitats and small labelled coloured disks per section, used to identify replicate specimen tanks.

Specimens in the increased seawater temperature (rockpool) treatments were removed from their overnight holding tanks every morning at 10:00 and placed into 1000 L heated seawater tanks set to 20 °C, then moved to 25 °C and 30 °C after increments of two hours each (Fig. 3A) to approximate natural gradual solar influence on rockpool temperatures during a heatwave event. After a final two hours in the 30 °C seawater tank, the specimens were immediately returned to their overnight holding tank at 15 °C to replicate an incoming tide. Specimens were left for ~30 min before inspection for inactivity/mortality, tanks cleaned and algal-covered pebbles replaced, then returned back to the holding tank overnight. EnvLogger temperature loggers were placed within the 20 °C, 25 °C, and 30 °C heated tanks for the duration of the experiment, recording temperatures every 30 min to provide a record of the actual seawater temperatures experienced by specimens in the experiment in simulated rockpool habitats.

A.3.3. Simulated cold spell conditions

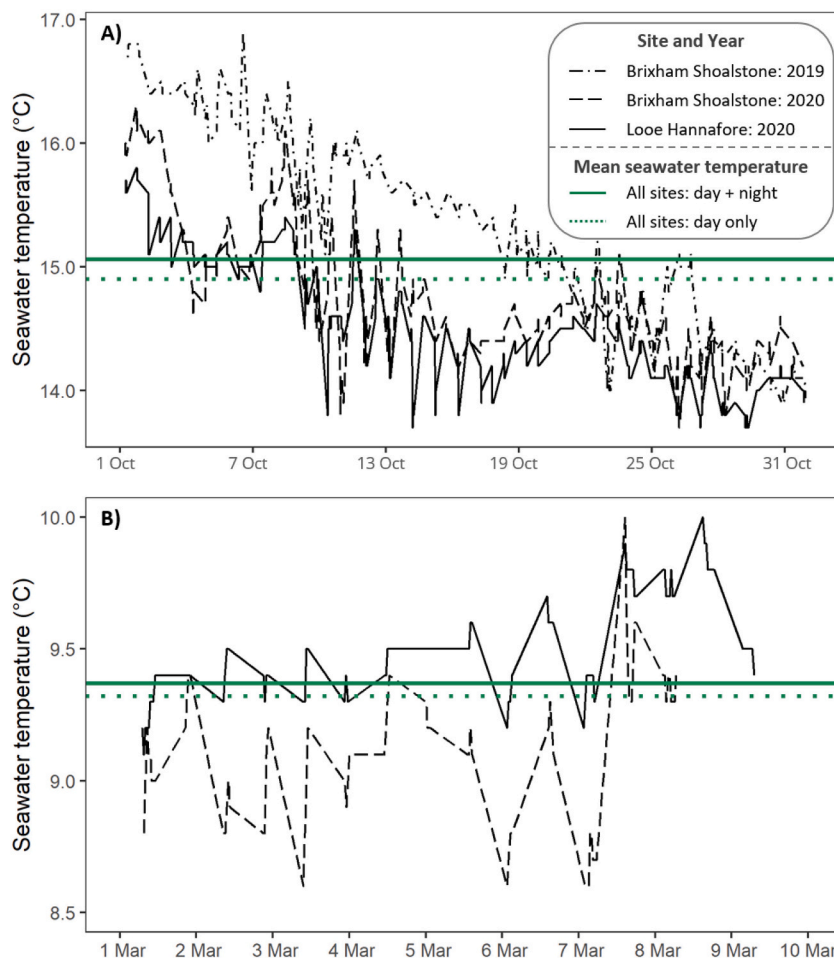
Minimum low-tide winter air and sea temperatures, taken from EnvLogger temperature loggers deployed on midshore rocky intertidal exposed bedrock and in rockpools at both Brixham Shoalstone and Looe Hannafore between 2020 and 2021, were used as target air (1.2 °C) and seawater (2.5 °C) temperatures for decreased winter cold spell treatments in this experiment (Table 1). Specimens in the decreased air temperature (boulderfield) treatment were removed from their overnight seawater holding tank each morning of the experiment, placed onto raised plastic gridded platforms within two plastic tanks in a temperature controlled room, with cooling fans set at 6 °C that resulted in air temperatures ~7 °C (Fig. 3B). After two

hours, a 14 L bucket-full of 5.5 °C (± 0.5 °C) seawater was emptied equally into the two plastic tanks, followed by ~ 11 L of ice, and the cooling fans lowered to 4 °C. The gridded platforms prevented contact of the replicate tanks with either the ice or 5.5 °C seawater to avoid freezing. Specimens in their replicate tanks remained on these platforms for four hours to allow a gradual decrease in air temperatures, caused by a combination of the lowered cooling fan temperatures and melting ice below the platforms. After a total of six hours in the temperature-controlled room, specimens in their replicate tanks were immediately returned to their overnight holding tanks to simulate an incoming tide. After ~ 30 min, specimens were then individually inspected for inactivity/mortality and returned again to their respective replicate tanks within the holding tanks until the following morning.

Specimens within their replicate tanks in the decreased seawater (rockpool) temperature treatment were removed from their overnight holding tanks each morning and immediately submersed into a separate 1000 L seawater tank set to 6 °C, where they remained for two hours (Fig. 3B). After this time, all replicate tanks were removed from the 6 °C seawater tank and randomly dispersed between four large plastic tanks in the temperature-controlled room (cooling fans set to 4 °C) that were each filled with ~ 26 L of 5.5 °C (± 1 °C) seawater. Pre-frozen domestic freezer blocks were evenly distributed amongst the large plastic tanks, where the replicate tanks were then left for four hours to allow the seawater to gradually decrease down to target temperatures of 1.5–2.5 °C. Although aquarium bubblers would have aided water circulation within these tanks, these were not available for use within these decreased temperature tanks. After four hours in the temperature-controlled room, specimens in their replicate tanks were immediately submersed into their overnight seawater holding tank to replicate an incoming tide. After ~ 30 min of submersion, specimens were then individually inspected for inactivity/mortality, then returned again to their respective replicate tanks within the overnight seawater holding tank until the following day.

Since two large plastic tanks separated the replicate tanks for the decreased air temperature treatment, two EnvLoggers were placed into two randomly chosen replicate tanks on a daily basis, placed separately into each of the larger plastic tanks. For the rockpool decreased temperature treatment, four EnvLoggers were separated into each of the large plastic tanks, placed into empty replicate tanks and set to record seawater temperatures every 10 min. A single EnvLogger temperature logger was placed in the temperature-controlled room on a bench above the decreased air temperature (boulderfield) specimen replicate tanks to provide a long-term record of the air temperatures experienced during the nine-day cold spell experiment. This was mainly used to check that the cooling fans were working as expected and to record air temperatures experienced by specimens should any technical / human errors occur with the decreased air temperature (boulderfield) treatment Envloggers.

A.4. Envlogger seawater tide-in temperatures

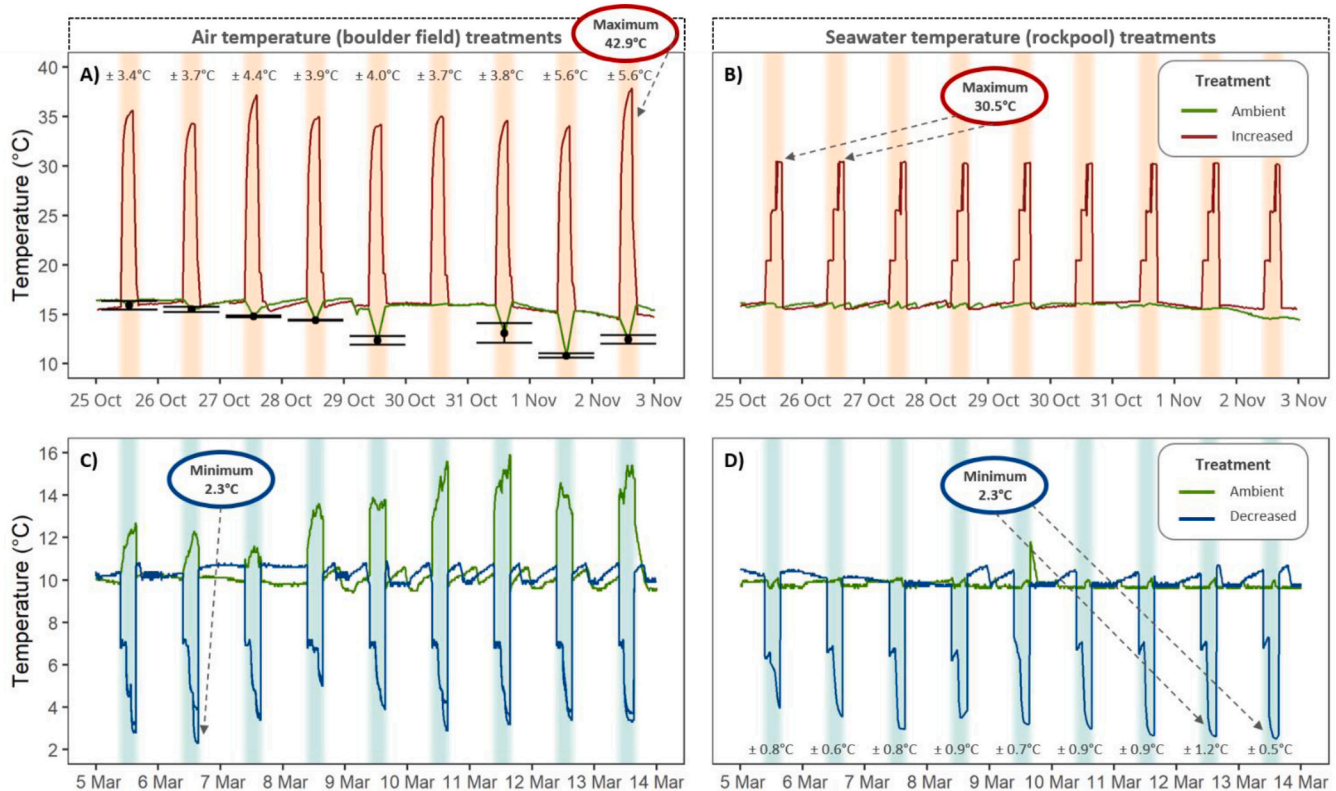


Appendix 7.4. Seawater temperatures 1–2 h either side of high tide, recorded by shaded Envlogger temperature loggers (electricblue.eu) recording every 30 min in the months of (A) October and (B) during the first 10 days of March deployed midshore on intertidal bedrock at both Brixham Shoalstone, South Devon (50.4013, -3.4960), and Looe Hannafore, South Cornwall (50.3411, -4.4598). Legend on plot (A) identifies linetypes according to site and year of temperature data for both plots, in addition to mean seawater temperature for day and night (dotted green line) and mean seawater temperature for daylight hours only (solid green line) for all

temperature data shown on each plot. Looe data for 2019 are not shown due to technical issues with the field logger, whilst limited temperature data for March 2020 (B) are available due to the subsequent loss of loggers at both sites after the data were downloaded on the 8th and 9th March 2020 at Brixham and Looe respectively.

A.5. Experimental treatment temperatures

The maximum temperatures reached within the heatwave thermal experiment were 42.9 °C for the extreme air (boulderfield) and 30.5 °C for the extreme seawater (rockpool) temperature treatments (Fig. 7.5.1), very closely matching the highest air (43.7 °C) and seawater (30.4 °C) temperatures recorded by in situ loggers at both Brixham Shoalstone and Looe Hannafore since 2019 (Table 1). The minimum temperatures reached within the cold spell thermal experiment both fell to 2.3 °C for the extreme air (boulderfield) and extreme seawater (rockpool) temperature treatments separately, approximating to the respective minimum air (1.2 °C) and seawater (2.5 °C) temperatures recorded by in situ loggers at Looe Hannafore in 2021 (Table 1). Increases in maximum daily ambient air temperature within the cold spell experiment occurred over the nine-day experimental period between 5th and 13th March 2022 (Fig. 7.5.1). This resulted in ‘simulated tide-out’ air temperatures ranging from a daily maximum of 11.6 °C on 7th March to 15.9 °C on the 11th March. These short-term increases in ambient air temperatures are a result of exposure to natural outside air temperatures within the Marine Biological Association’s main Seawater Hall, which provided natural daily variability experienced by these specimens on local shores to the laboratory so were in keeping with seasonally ambient conditions, rather than extreme cold spell events.



Appendix Fig. 7.5.1. Temperatures experienced by specimens during simulated extreme heatwave (A & B) and cold spell (C & D) events for air (A & C) and seawater (B & D) temperature manipulation experiments. Vertical coloured background blocks show daily simulated tide-out periods. In situ field Envlogger temperature data are shown using point data (black circles \pm standard error). Increased/decreased treatments in (A & D) show daily mean maximum/minimum temperatures across multiple temperature loggers (increased air = 8, decreased seawater = 4) with range labelled above/below. Decreased air temperatures were recorded by two temperature loggers, therefore both are shown (C).

A.6. Daily inactivity counts

Appendix 7.6

Inactivity counts split daily by size class (nr = new recruits, y1 = year 1+ recruits) for both the heatwave and cold thermal experiments, separated by habitat type (boulderfield, rockpool), temperature treatment (ambient, increased/decreased) and species (*Phorcus lineatus*, *Littorina littorea*, *Steromphala umbilicalis*, *Steromphala cineraria*).

	Thermal experiment		Heatwave									Cold spell										
	Temp. treatment	Species	Day 1 nr/ y1	Day 2 nr/y1	Day 3 nr/ y1	Day 4 nr/y1	Day 5 nr/ y1	Day 6 nr/y1	Day 7 nr/y1	Day 8 nr/y1	Day 9 nr/y1	Day 1 nr/ y1	Day 2 nr/y1	Day 3 nr/ y1	Day 4 nr/y1	Day 5 nr/ y1	Day 6 nr/y1	Day 7 nr/y1	Day 8 nr/y1	Day 9 nr/y1		
Air (boulderfield) experiment	Ambient	<i>P.lineatus</i>	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	
		<i>L.littorea</i>	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
		<i>S.umbilicalis</i>	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
		<i>S.cineraria</i>	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0
		<i>P.lineatus</i>	1 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
	Increased/decreased	<i>L.littorea</i>	5 / 3	1 / 1	2 / 4	0 / 1	0 / 0	1 / 0	0 / 0	1 / 0	3 / 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
		<i>S.umbilicalis</i>	1 / 2	0 / 2	6 / 9	2 / 2	0 / 1	0 / 0	0 / 0	1 / 0	2 / 3	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
		<i>S.cineraria</i>	30 / 30	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
		<i>P.lineatus</i>	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
		<i>L.littorea</i>	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Seawater (rockpool) experiment	Ambient	<i>S.umbilicalis</i>	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	
		<i>S.cineraria</i>	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	
		<i>P.lineatus</i>	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	
		<i>L.littorea</i>	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
	Increased/decreased	<i>S.umbilicalis</i>	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
		<i>S.cineraris</i>	0 / 0	0 / 0	1 / 2	2 / 0	0 / 0	0 / 0	0 / 2	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0

A.7. Pairwise comparisons of heatwave aerial cumulative survivorship

Appendix 7.7

Pairwise comparison results from permutational pairwise tests using Euclidean distance matrices and bonferroni adjustment, showing differences in arcsine-transformed cumulative survivorship percentage for 'species' as a fixed factor. Results are shown separately for simulated boulderfield and rockpool increased temperature treatments in the heatwave thermal experiment. Significant p-values are emboldened and cells highlighted grey. All NA results for pairwise comparisons between species in the ambient temperature treatments, and between *P. lineatus* and *S. umbilicalis* in the rockpool increased temperature treatment, is a result of full survivorship (100%) in both species, meaning this pairwise result was not calculable.

		Boulderfield simulated habitat			Rockpool simulated habitat		
		<i>Littorina littorea</i>	<i>Steromphala umbilicalis</i>	<i>Steromphala cineraria</i>	<i>Littorina littorea</i>	<i>Steromphala umbilicalis</i>	<i>Steromphala cineraria</i>
Increased temperature treatment	<i>Phorcus lineatus</i>	0.030	0.006	0.006	1.000	NA	0.070
	<i>Littorina littorea</i>	-	0.870	0.006	-	1.000	0.215
	<i>Steromphala umbilicalis</i>	-	-	0.006	-	-	0.050
Ambient temperature treatment	<i>Phorcus lineatus</i>	NA	NA	NA	NA	NA	1.000
	<i>Littorina littorea</i>	-	NA	NA	-	NA	1.000
	<i>Steromphala umbilicalis</i>	-	-	NA	-	-	1.000

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Further reading

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